Relationship Between Color Discrimination and Neural Responses in the Inferior Temporal Cortex of the Monkey

Takehiro Matsumora,1,2 Kowa Koida,1,2 and Hidehiko Komatsu1,2

1Division of Sensory and Cognitive Information, National Institute for Physiological Sciences and 2Department of Physiological Sciences, The Graduate University for Advanced Studies, Okazaki, Aichi, Japan

Submitted 12 May 2008; accepted in final form 12 October 2008


INTRODUCTION

In the cerebral cortex of the monkey, color information is transmitted along the ventral visual stream, which includes areas V1, V2, and V4, until it ultimately reaches the inferior temporal (IT) cortex (Conway and Tsao 2006; Desimone et al. 1984; Fujita et al. 1992; Komatsu 1998; Komatsu et al. 1992; Maunsell and Newsome 1987; Tootell et al. 2004; Zeki 2005). Several studies have shown that lesionsing or cooling the IT cortex seriously impairs color discrimination (Buckley et al. 1997; Dean 1979; Heywood et al. 1995; Horel 1994; Huxlin et al. 2000); moreover, neural recording studies have shown that many neurons in the IT cortex selectively respond to specific colors (Desimone et al. 1984; Kobatake and Tanaka 1994; Koida and Komatsu 2007; Komatsu and Ideura 1993; Komatsu et al. 1992; Zeki 1996). These neurons are narrowly tuned to various hues and saturation of color and appear to be concentrated in several subregions of the IT cortex, including areas TE and TEO (Conway et al. 2007; Yasuda and Komatsu 2005; Yasuda et al. 2004). Although it is natural to assume that these color-selective neurons play important roles in color discrimination, there has been no study in which this issue was systematically examined.

Our aim in the present study was to quantitatively examine the relationship between the activity of color-selective TE neurons and color-discrimination behavior in the monkey. We have concentrated on TE, where neurons have large receptive fields including the fovea, and the recorded area is clearly distinct from the more posterior region in IT where color-selective neurons have been reported recently (Conway et al. 2007). To quantitatively examine the color-discrimination behavior, we trained monkeys to perform a color-judgment task in which they had to make fine discriminations of color. While they performed this task, we simultaneously recorded the monkeys’ color-discrimination behavior and the activity of single TE color-selective neurons. The color stimuli used for the task were tailored to the color selectivity of each isolated neuron under study, so that the neuron could provide sensory information useful for the performance of the task. We then analyzed the relationship between the neural responses and the monkeys’ behavior, using an ideal-observer analysis that has been used previously to study the relationship between neural activity and the perception of both motion and depth (Albrecht and Jägadeesh 2007; Britten et al. 1992; Nienborg and Cumming 2006; Parker and Newsome 1998; Purushothaman and Bradley 2005; Shadlen et al. 1996; Uka and DeAngelis 2003; Uka et al. 2005). Color is represented by the combination of hue and saturation and many IT neurons were selective for both. In the present study, we mainly focused on the relationships between neural and behavioral sensitivities to hue, which most prominently characterizes individual colors. Some IT neurons were selective exclusively for saturation; in those neurons the relationships between neural and behavioral sensitivities to saturation were examined.

We compared the color-discrimination threshold computed from the neural responses and the behavioral threshold and also computed the correlation between the trial-to-trial fluctuation in neural activity and the monkeys’ color judgment. We found that individual color-selective TE neurons are slightly less sensitive to the color difference than the whole animal and that, in general, each neuron weakly contributes to color discrimination. These findings suggest...
that a large population of color-selective TE neurons contributes to color discrimination behavior.

METHODS

Preparation of the monkeys

Two Japanese macaque monkeys (Macaca fuscata, one female weighing 5.5 kg, one male weighing 7.0 kg) were used for these experiments. Under sodium pentobarbital anesthesia, a sterile surgery was conducted to attach a stainless steel head holder to the top of the skull using dental acrylic and to implant an eye coil in one eye (Judge et al. 1980). More than 1 wk after the surgery, training on the color-judgment task was begun. It took 2–4 mo for each monkey to learn to do the task (initial training period). Once the monkeys’ performance of the task stabilized at a satisfactory level, a second surgery was conducted to place a recording chamber on the skull. The chamber was placed at a position where an electrode could be inserted vertically into the region around the posterior edge of the anterior middle temporal sulcus (amts) in area TE (Fig. 1), where previous studies have shown color-selective neurons are densely distributed (Koida and Komatsu 2007; Yasuda et al. 2004). The position of the amts was identified by magnetic resonance imaging (MRI) carried out before the surgery. Judging from the sulcal landmarks, this region is located in the middle of area TE. When we mapped the receptive fields of the recorded neurons, we found that they commonly had large receptive fields extending bilaterally and included the fovea, which is consistent with previous findings in area TE. More than 1 wk after the second surgery, recording sessions were begun. Throughout the study, the monkeys were deprived of water for about 16 h prior to each daily experimental session. The monkeys obtained liquid reward as they performed their task until they were satisfied. Over the weekends, the monkeys were provided with ample water. All procedures for animal care and experimentation were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals (1996) and were approved by the Institutional Animal Experimentation Committee.

Behavioral tasks and visual stimuli

During the experiments, each monkey was seated on a primate chair, to which its head was securely fixed with a head-holding device, and faced a color monitor at a distance of 76 cm. It then performed a simple visual-fixation task and a color-judgment task. While the monkey performed the visual-fixation task, we examined the color and shape selectivities of the recorded neurons. A color-judgment task was then used to examine the quantitative relationships between the monkey’s color judgment and the simultaneously recorded neural activity. In the following, we will first explain about the color-judgment task in detail and then briefly explain the fixation task and the procedures for the determination of color/shape selectivity.

COLOR-JUDGMENT TASK. The color-judgment task (Fig. 2A) started when the monkey gazed at a fixation spot (0.07-deg diameter, 60 cd/m²) presented at the center of the monitor (10 cd/m² gray background). After 500 ms, the fixation spot disappeared and a blank screen was presented for 350 ms, after which a color stimulus (sample color) was presented at the center of the monitor for 500 ms. When the sample color stimulus was turned off, two white stimuli (choice targets, 20 cd/m²) with the same shape and size as the sample color stimulus appeared to the left and right of the fixation position (x = ±5 deg, y = 0 deg). The monkeys were required to make a two-alternative forced choice (2AFC) of the targets and were rewarded when they made a saccade to either one of the choice targets that was associated with the sample color. The monkeys had to maintain fixation within a ±1-deg window until the choice targets were presented. If the eye position deviated from the window, the trial was aborted and the intertrial interval was started. The monkey’s response was judged to be correct if the endpoint of the saccade was within a ±1.5-deg window around the correct choice target. Eye position was monitored using the scleral search coil method (Robinson 1963).

The sample color set consisted of seven isoluminant colors (20 or 5 cd/m²). In most instances, we used color stimuli that were brighter than the background (20 cd/m²); however, when the recorded neurons clearly preferred darker colors or blue (seven neurons recorded from monkey R), we used colors darker than the background (5 cd/m²). The chromaticity coordinates of the seven sample colors were aligned mainly on the edge of the color triangle, at equal intervals on the International Commission on Illumination (CIE)-xy chromaticity diagram, or around white (D65) (Fig. 5). The stimulus color was measured and calibrated using a spectrophotometer (Photo Research PR-650). The left choice target was associated with one end of the sample color set (color #1 or #7) and the right choice target with the opposite end. At the beginning of training on a given sample color set, the choice targets were assigned the #1 and #7 colors and the monkeys learned the association between the color and the direction of choice. Once that was learned, the colors of the choice targets turned to white. The monkeys then had to judge whether the sample color was more similar to color #1 or to color #7 and make a saccade to the associated choice target. When the sample color was more similar to color #1 (colors #1, #2, or #3), the monkeys were rewarded when they made a saccade to the choice target associated with color #1 (color #1-choice); when the sample color was more similar to color #7 (colors
Initially, the color selectivity of the recorded neuron was determined in a fixation task (see FIXATION TASK for details) and sample color sets for the subsequent discrimination task were tailored to the color selectivity of that neuron. The center color in the sample color set (color #4) was selected as the point where neural responses sharply changed; in other words, the point where the tuning curve had a large slope. This was because it has been shown that sensory neurons exhibit the greatest ability to discriminate around the point where the tuning curve is steepest (Purushothaman and Bradley 2005; Schopou et al. 2001). The range of the sample color set was made to be about two- to threefold larger than the color-discrimination threshold obtained during the initial training period, but was adjusted according to the monkey’s performance during each daily session. Once the data recording from a given neuron was started, the sample color set was fixed. For the sake of convenience, in the following text the color at the end of the sample color set nearest the preferred color will be referred to as “sample color #7,” whereas the color at the opposite end of the sample color set will be referred to as “sample color #1.” For each neuron, the left and right choice targets were arbitrarily and randomly assigned to either color #1 or color #7 of the sample color set. After determination of the selectivity of each neuron, the monkeys had to learn the association between the direction of saccade and each of the two end colors (#1 and #7). It took about 150–250 trials (or 20–30 min) for the monkeys to become accustomed to the new sample color set and achieve stable performances with >75% correct responses. Finally, we began recording the behavioral performance and neuronal activity. During the recording, each sample color was presented from 18 to 286 times (for monkey Y, range = 27–286, median = 107; for monkey R, range = 18–282, median = 105).

FIG. 2. Color-judgment task. A: time course of the color-judgment task. This task started when the monkey gazed at a fixation spot presented at the center of the monitor. After 500 ms, the fixation spot disappeared and a blank screen was presented for 350 ms. A color stimulus (sample color) was then presented at the center of the monitor for 500 ms. When the sample color stimulus was turned off, 2 white stimuli (choice targets) appeared to the left and right of the fixation position. The monkeys were rewarded for making a saccade to either one of the choice targets that was associated with the sample color (see METHODS for more details). B: color selectivity of an example neuron and the sample color set used for this neuron. These are shown in the same format used in Fig. 3, B–D. C: enlarged view of the sample color set shown in B. D: psychometric function constructed from the monkey’s behavior during the same recording session. The proportion of the responses in which the monkey chose the target associated with sample color #7 (color #7-choice) is plotted for each sample color. Data points were then fitted with a logistic function (curved line). The psychometric threshold was calculated as the interval between the points where the color #7-choice becomes either 80 or 20%. The psychometric threshold obtained during this recording session is compared with the sample color set in C.

#5, #6, or #7), they had to make a saccade to the other choice target (color #7-choice). When the intermediate sample color (color #4) was presented, the monkeys were randomly rewarded 50% of the time, regardless of the direction of the saccade. After the monkey made a saccade to the choice target, the color of the choice target was changed from white to the associated color (either color #1 or color #7) for 250 ms (or 100 ms in some early sessions with monkey Y) as feedback.

At the end of the initial training period when the basic training on the color-judgment task was finished, we measured color-discrimination thresholds at several locations on the chromaticity diagram: three positions at each edge of the color triangle and those around the white point (D65). Color-discrimination thresholds were determined for each of these color sets. After measurement of the discrimination threshold at various locations on the chromaticity diagram was complete, neural recording experiments were begun.

During the neural recording experiments, the daily session consisted of the following three steps: 1) examination of the color selectivity of the recorded neuron during the fixation task and determination of the sample color set for the color-judgment task; 2) training in a color-judgment task with this new sample color set until a good and stable performance was achieved; and 3) simultaneous recording of the monkey’s behavior and neural responses while it performed the color-judgment task. In the following, each of these steps will be explained in more detail.
respond to color stimuli with these simple geometrical patterns (Koida and Komatsu 2007; Komatsu and Ideura 1993). All shapes had the same area (3.14 deg²). The size of the bar stimulus was 1.02 × 3.07 deg. The horizontal extent of the other shapes ranged from 1.77 to 2.69 deg.

The shape that induced the strongest response in each neuron was used to test the color selectivity and the preferred color was used to test the shape selectivity. To do this, we explored the optimum parameters for each neuron as follows. We first tested color selectivity using a particular shape (usually a disk). If a response was obtained, we tested shape selectivity using the color that evoked the strongest response. We repeated this cycle until we found the optimal combination of color and shape and defined them as the preferred color and shape. If we failed to drive the neuron using these parameters for each neuron as follows. We first tested color selectivity using a particular shape (usually a disk). If a response was obtained, we tested shape selectivity using the color that evoked the strongest response. We repeated this cycle until we found the optimal combination of color and shape and defined them as the preferred color and shape. If we failed to drive the neuron using these procedures, we advanced the electrode to examine another neuron. To quantitatively determine the color and shape selectivities, each visual stimulus was presented more than five times.

Recording

The activities of single neurons were recorded extracellularly from three hemispheres using tungsten microelectrodes (2–3 MΩ, FHC) that were held by a micromanipulator (Narishige MO951) and inserted vertically into the brain through a stainless steel guide tube attached to a grid that was fixed within the recording chamber. The grid had holes placed at 1-mm intervals, so that the electrodes were inserted at 1-mm intervals. In each hemisphere, recordings were made in two stages. In the first stage, we mapped the distributions of color-selective neurons around the posterior end of the ams by inserting the electrode into a different location each day. In the second stage, a guide tube was implanted chronically in the brain, such that the tip of the guide tube was several millimeters above the target site. A thinner electrode was then advanced through the guide tube every day to sample neural activity from the same site. Neural activity was amplified, sampled at a rate of 25 kHz, and stored on a hard disk. We recorded only well-isolated single neurons. While recording, we used a discriminator to detect spike discharge from a single neuron, after which we would quantitatively determine the color selectivity of that neuron. Color stimuli for the color-judgment task were selected based on this on-line analysis. For off-line analysis, the activity of single neurons was isolated using custom software based on the template-matching algorithm. We also recorded eye positions at a sampling rate of 1 kHz.

Data analysis

BEHAVIORAL DATA: PSYCHOMETRIC FUNCTION AND PSYCHOMETRIC THRESHOLD. While the monkey was performing the color-judgment task in each recording session, we simultaneously recorded the activ-

FIG. 3. Test of color selectivity during the fixation task. A: color stimulus set used to test color selectivity. These include 15 colors that uniformly distribute across the color triangle on the CIE-xy chromaticity diagram plus white (D65). The chromaticity coordinates of these 16 colors are shown as crosses. R, red; G, green; B, blue; W, white. B: color selectivity of an example neuron shown on a bubble plot. Circle diameters represent the response magnitudes to the respective colors and the circles are plotted at the chromaticity coordinates of the colors. Open circles represent excitatory responses, dark circles inhibitory responses. A contour plot connects the positions where the response magnitudes become 75, 50, and 25% of the maximum response. Seven linearly aligned small dots indicate the sample color set used in the color-judgment task for the same neuron. C and D: color selectivity and sample color sets for 2 other example neurons. The format is the same as in B.

FIG. 4. Color and shape selectivities of all 87 neurons analyzed in the color-judgment task. A and C: distributions of the color selectivity (A) and shape selectivity (C) indexes. The selectivity index becomes >1 when a neuron is suppressed by a stimulus and the minimum response falls below the background discharge rate. B and D: distributions of the color sparseness (B) and shape sparseness (D) indexes. Triangles indicate the means. Shapes used in the experiments are shown as an inset in C.
ity of a single neuron and the monkey’s behavior. To evaluate the behavioral performance during the recording session, we constructed a psychometric function, an example of which is shown in Fig. 2D, as follows. The proportion of trials in which the monkey chose the target associated with color #7 (color #7-choice) was plotted for each sample color. Then to obtain the psychometric function, the data were fitted with a logistic function using the following equation

\[ \text{Logistic Function} = \frac{1}{1 + \exp[-\alpha(x - \beta)]} \]  \hspace{1cm} (1)

where \( x \) represents the sample color number (#1–#7), \( \alpha \) corresponds to the slope of the function that represents the sensitivity to the difference in color, and \( \beta \) represents the color that yields 50% color #7-choice. Parameters \( \alpha \) and \( \beta \) were estimated using a nonlinear regression algorithm (nlmfit in Matlab). We then computed the \( x \) values for the points at which the color #7-choice was either 80 or 20% (horizontal dashed line in Fig. 2D) on the fitted curve and the interval between these two \( x \) values was converted to the distance on the CIE-xy chromaticity diagram. That distance was defined as the psychometric color-discrimination threshold (Fig. 2, C and D).

COLOR AND SHAPE SELECTIVITY. The color and shape selectivities of each neuron were determined based on the responses to the 15 colors brighter than the background or 16 colors darker than the background and the 11 shapes recorded during the fixation task. In this and the following analysis, mean spike rates recorded between 50 and 550 ms after the onset of the sample color minus those recorded between 300 and 0 ms before the onset were defined as the neural response to that stimulus unless otherwise noted. To evaluate the degree of color or shape selectivity, a selectivity index was calculated as 1 − Rmin/Rmax, where Rmin represents the minimum of the mean responses to the 16 (or 15) colors or 11 shapes, and Rmax represents the maximum of the mean responses. To evaluate the sharpness of the color or shape selectivity, a sparseness index (Rolls and Tovee 1995) was calculated using the following equation

\[ \text{Sparseness Index} = \frac{1}{n} \left( \sum_{i=1}^{n} R_i \right)^2 \]  \hspace{1cm} (2)

where \( n \) represents the number of stimuli tested (15 or 16 for color, 11 for shape) and \( R_i \) represents the magnitude of the response to each stimulus. If because of suppression the response magnitude was negative, it was replaced by 0. The sparseness index ranged between 1/n and 1. If the selectivity was very sharp and only one stimulus evoked a response, the index value became 1/n (0.06 for color, 0.09 for shape). As the selectivity became broader, the index value became larger until it reached 1 when all stimuli evoked the same responses.

NEUROMETRIC FUNCTION AND NEUROMETRIC THRESHOLD. To evaluate the neural sensitivity to sample colors, we constructed neurometric functions that reflected the proportion of the color #7-choices (color #7-choice ratio) based on the activities of the individual neurons. To compute a neurometric function, we applied a “neuron–antineuron model” (Britten et al. 1992; Ditterich et al. 2003; Shadlen et al. 1996), which assumes a pair of neurons: a “pref-neuron,” which corresponds to the single neuron actually recorded, and an “antineuron.” Within the range of the sample color set used (#1–#7), the pref-neuron and the antineuron have exactly the same color tuning profile, except that the tuning curves are mirror-reversed with respect to one another at color #4 (Fig. 7A). The probability of the color #7-choice for each sample color was then calculated using receiver-operating-characteristic (ROC) analysis, assuming that the ideal observer makes a judgment based on the response distribution of both the pref- and antineurons. This probability is also referred to as the ROC value. We then constructed a neurometric function that expresses the color #7-choice (or ROC value) as a function of the sample color. This function represents the performance of an ideal observer who relies on the activity of the recorded neuron. It should be noted that, in our neurometric function, the color #7-choice for sample color #4 is always 0.5 because the responses of the pref- and antineurons are the same and the left and right halves of this function are point reflections of each other. The neurometric function was then fitted with the logistic function, after which the neurometric threshold was calculated from the fitted curve using the same procedure used to calculate the psychometric threshold.

To ensure a reliable conclusion, we only analyzed neurons that met all of the following criteria: the neuron must have shown significant color selectivity (ANOVA, \( P < 0.05 \)) during the fixation task; the maximum response must have been >10 spikes/s; and neural responses to sample colors #1 and #7 must have been significantly different (\( t \)-test, \( P < 0.05 \)). We recorded 109 single neurons that responded to our visual stimuli. Of those, 94 satisfied all three of the aforementioned criteria. From these neurons, we excluded those whose responses clearly declined after the start of the color-judgment task (two neurons) and those whose color selectivity tested during the color-judgment task was not consistent with that during the fixation task (three neurons). Moreover, if a monkey’s performance with the two end colors (#1 and #7) was <80% during the recording of a neuron (two neurons), that neuron was excluded from the sample because the monkey did not perform the task adequately. As a result, 87 neurons remained for detailed analysis of the quantitative relationship between neuronal activity and the color-discrimination behavior.

We also used the \( \chi^2 \) test to evaluate the goodness of fit of the psychometric or neurometric function by comparing the quality of the fit to that of the mean response alone (Britten and Newsome 1998). When there was no significant improvement in fit (\( P < 0.05 \)), the data were rejected from further quantitative analysis.

CHOICE PROBABILITY. To assess the correlation between trial-to-trial fluctuations in the responses of IT neurons and the color judgments made by the monkey, we computed the “Choice Probability (CP)” (Britten et al. 1996). On the one hand, the monkey’s color judgment, even to the same sample color, fluctuated across trials. [This was more pronounced for intermediate colors (#3, #4, or #5) in the sample color set and less so for end colors (#1 and #7).] On the other hand, neural responses to the same color also showed trial-to-trial fluctuations. If neural activity affects color judgment, we would expect that fluctuation in the neural response would correlate with the monkey’s color judgment; for example, in a trial in which the neural response is relatively strong, the expectation would be that the monkey would tend to make the color #7-choice. To evaluate the degree of correlation, we first categorized the responses of the neuron under study to a given sample color into two groups, based on the monkey’s color judgments in the trials, and constructed a distribution of the spike counts in each trial for each of these two groups. The separations between the response distributions of the two groups were then quantified using the same procedures used for ROC analysis. The resultant value is referred to as the CP and ranged from 0 to 1. If there was a positive correlation between neural activity and the monkey’s color judgment, the CP would be >0.5, and if there was negative correlation, it would be <0.5. The CP for each sample color was computed only when the monkey made both color #7-choices and color #1-choices >10 times. We also used a permutation test to determine whether the CP for each neuron differed significantly from 0.5. In that test, CP was recomputed after the correspondence between the neural response and the trial number was randomly shuffled. This process was repeated 2,000 times to generate a probability distribution for CP that was independent of the original trial-to-trial relationship between neural activity and the monkey’s color judgment, but was calculated from
those same two distributions. If the CP from the actual data were outside the central 95% of the distribution, it was considered to be significantly different from 0.5.

For each individual neuron, a CP could be computed for each sample color. To obtain a representative CP value for each neuron, trials used in the calculation of the CP for different sample colors were merged and a CP was calculated from the new population. This CP is referred to as the “Grand Choice Probability (GCP)” (Britten et al. 1996). Because the mean and variance of the responses to each sample color were different, neural responses to each sample color were z-scored before combining the data.

**RESULTS**

**Color and shape selectivity of TE neurons**

We analyzed the relationship between neuron activities and the color-discrimination behavior in 87 single neurons (59 from monkey Y and 28 from monkey R). Figure 3, B–D shows the color selectivity of three example TE neurons examined during the fixation task. The neurons in Fig. 3, B and C had sharp color tuning to magenta (B) or cyan (C), whereas that in Fig. 3D had broader color tuning to yellow. We computed a color selectivity index and color sparseness index for each neuron (see Methods), and the distributions of these indexes are shown in Fig. 4, A and B, respectively. The mean of the color selectivity indexes was 1.11, whereas that of the color sparseness indexes was 0.43, indicating that the recorded TE neurons tended to have strong and sharp color selectivity. Figure 4, C and D shows the distributions of the shape selectivity and shape sparseness indexes, respectively. The mean of the shape selectivity indexes was 0.58, whereas that of the shape sparseness indexes was 0.9, indicating that the shape selectivity of these neurons tended to be broad with our stimulus set.

**Monkey behavior during a color-judgment task**

To examine the relationship between neural activity and a monkey’s ability to discriminate color, we recorded neural activity while the monkeys performed a color-judgment task (Fig. 2A). Figure 2, B and C shows the sample color set used to run the task with an example neuron. The color selectivity of this neuron during the fixation task is seen in Fig. 2B (responses during the color-judgment task are seen in Fig. 6). The sample color set consisted of seven isoluminant colors that were tailored to the color selectivity of the recorded neuron, so that it was positioned where the color tuning had a large slope (Fig. 2B; see also Fig. 3, B–D).

Figure 2D summarizes the behavioral performance during the recording of this neuron. A sample color was presented while the monkey maintained fixation. The monkey had to judge whether the sample color was more similar to color #1 or to color #7 and make a saccade to the associated choice target that appeared after the sample color was turned off. When the sample color was more similar to color #1, the monkey had to make a saccade to the choice target associated with color #1 (color #1-choice) and when the sample color was more similar to color #7, it had to make a saccade to the other choice target (color #7-choice). Color #7 corresponds to the end color of the sample color set on the side of the preferred color of the recorded neuron, which in this case was in the reddish region of the chromaticity diagram. In most cases psychometric functions took the form of a sigmoid curve (Fig. 2D; see also Fig. 5, C and D, insets, which show typical examples recorded at different parts of the chromaticity diagram). The psychometric threshold for color discrimination was determined after fitting the psychometric function with a logistic function (Fig. 2D; and see Methods, Eq. 1). The fit could be rejected for only one of the 87 psychometric functions in our data set ($\chi^2$ test, $P > 0.05$) and the thresholds for the remaining 86 cases were used for further analysis. It can be seen that the monkey was able to discriminate within a very narrow range of colors. In some cases (24 neurons), there were only a small number of data points ($n < 3$) within the stimulus range between 20 and 80% for the color-#7 choice. To test whether this influenced the results, we conducted an additional behavioral test in both monkeys using two stimulus sets with different stimulus intervals. One stimulus set was basically the same as that used in the original experiment and contained seven sample colors with equal intervals. In another stimulus set, the entire range of the sample color was the same as the original one, but we increased the number of colors contained in the stimulus set to nine so that the interstimulus interval was smaller. We then compared the psychometric functions obtained using these two sample color sets. We found that the resulting psychometric functions were nearly identical. There was no statistically significant difference between the thresholds obtained in these two conditions (bootstrap analysis, $P > 0.1$). This means it is highly unlikely that our measurements in the present study overestimated or underestimated the psychometric threshold.

The ranges of the sample color sets and the resultant psychometric thresholds recorded in all of the experiments are shown in Fig. 5. Figure 5, A and B shows the ranges of the sample color sets used for each neuron recorded from monkeys Y (A) and R (B). The head and tail of each arrow represent the chromaticity coordinates of colors #7 and #1, respectively. Because neurons with similar color tuning were recorded during several recording sessions, and the psychometric functions were determined for colors defined by the neural recordings, the psychometric curves for color discrimination in a given region of color space were determined multiple times over the course of the experiment. When the arrows overlapped, the one recorded more recently was shifted outward in a direction orthogonal to the edge of the color triangle. Figure 5, C and D shows the ranges of psychometric thresholds plotted as before. These ranges were shorter than the ranges of the sample color sets used for the experiment, as we intended (mean = 33%, SD = 10%).

In both monkeys, there was a tendency for the psychometric thresholds to be short around white and red and comparatively long around cyan. This variation roughly corresponds to that of the psychometric color-discrimination threshold in humans (MacAdam 1942; Newhall et al. 1957; Romero et al. 1993; Wright 1941) and reflects the fact that the CIE-xy chromaticity diagram is not a uniform color diagram. In other words, the distances in this diagram do not correspond to perceptual distances. This will be more thoroughly analyzed in relation to the variation in neural sensitivities in the following section.

As described earlier, more recent data are plotted farther away from the edge of the color triangle in Fig. 5, C and D. We did not find any systematic change in the color-discrimination threshold that was dependent on the time at which the data were recorded. This means that discrimination behavior in
response to similar color stimuli was quite stable over the entire course of the experiment.

Neural sensitivity to sample colors

To compare a single neuron’s ability to discriminate color with that of the monkey during a color-judgment task, we evaluated the neurometric threshold based on the neuronal responses to the sample colors. Figure 6 shows the responses of the same neuron characterized in Fig. 2 to each sample color during the color-judgment task displayed in raster plots (top) and in peristimulus time histograms (PSTHs) (bottom). This neuron selectively responded to reddish colors (Fig. 6). Consistent with the color selectivity determined in the fixation task, more reddish colors (colors with a larger color number) induced stronger responses. Based on these neural responses, we constructed a neurometric function and computed the neurometric threshold as a measure of the performance of this neuron in the color-judgment task. To construct the neurometric function, we applied a version of the “neuron–antineuron model” (see METHODS), in which target selection was made by comparing the responses of a pref-neuron and an antineuron. Figure 7A shows the actually recorded responses of the pref-neuron (solid curve) and the hypothetical responses of the antineuron (broken curve) to each sample color. ROC analysis was conducted to compute the probability that the ideal observer makes the color #7-choice based on the frequency distributions of the trial-to-trial spike counts for both the pref-neuron and antineuron. For this neuron, the ROC value was near 0 for color #1 and gradually increased toward color #7. Based on these values, we constructed a neurometric function that shows the ROC value for each sample color (Fig. 7B). Like the psychometric function, the neurometric function took the form of a sigmoid curve. In the same way that we calculated the psychometric threshold, we determined the neurometric threshold after the neurometric function was fitted with a logistic function (METHODS, Eq. 1). The fit was rejected for only one of the 86 neurometric functions in our data set (χ² test, P > 0.05) and the thresholds for the remaining 85 cases were used for further analysis.

Figure 8, A–F shows neurometric functions (solid curves) for six example neurons and simultaneously recorded psychometric functions (broken curves). Neurons in Fig. 8, A–C were recorded from monkey Y; those in Fig. 8, D–F were from monkey R. For some neurons, such as those in Fig. 8, A and D, the slopes of the neurometric functions were steeper than those of the psychometric functions, indicating that these single neurons have a greater sensitivity to the sample colors than the monkeys; in other words, they have a greater ability to discriminate color. For other neurons, such as those in Fig. 8, B and E, the neurometric functions were nearly identical to the psychometric functions, indicating that the color sensitivities of the single neurons are comparable to those of the monkeys. Moreover, for still other neurons, such as those in Fig. 8, C and F, the slopes of neurometric functions were less steep than those of the psychometric functions, indicating that these
Figure 8G shows the relationship between the neurometric threshold and the simultaneously recorded psychometric threshold. Both thresholds were determined based on the fitted logistic functions. We excluded two neurons from this graph because their neurometric thresholds were more than twice as long as the width of the sample color set, which would likely make the estimates unreliable. A majority of the data points lay below the diagonal line where the neurometric and psychometric thresholds are the same. The histogram in the inset illustrates the difference between the two thresholds on a log scale and shows that, on average, the neurometric threshold was larger than the psychometric threshold (triangle in the inset). Indeed, the average neurometric threshold (monkey Y, mean = 0.0268; monkey R, mean = 0.0305; both, mean = 0.0279) for the entire population of recorded neurons was significantly larger than the psychometric threshold (triangle in the inset). The histogram in the inset illustrates the difference between the two thresholds on a log scale and shows that, on average, the neurometric threshold was larger than the psychometric threshold (triangle in the inset). Indeed, the average neurometric threshold (monkey Y, mean = 0.0268; monkey R, mean = 0.0305; both, mean = 0.0279) for the entire population of recorded neurons was significantly larger than the psychometric threshold (monkey Y, mean = 0.0159; monkey R, mean = 0.0262; both, mean = 0.0186; Wilcoxon test, $P < 0.0001$), with an average neuronal-to-psychophysical threshold ratio of 1.502 (monkey Y, mean = 1.685; monkey R, mean = 1.168). In 11 of the 83 neurons analyzed, the neurometric threshold exceeded the range of the sample color set and was determined based on extrapolation. No psychometric threshold was based on extrapolation. When the 11 neurons whose responses were extrapolated to compute neurometric thresholds were excluded from the analysis, the results were essentially the same and the average neurometric threshold for the remaining neurons continued to be significantly larger than the psychometric threshold (Wilcoxon test, $P < 0.01$). In sum, it thus appears that the performance of individual TE color-selective neurons during a color-judgment task was generally not quite as good as that of the monkey, although some neurons showed an ability to discriminate color that was comparable or superior to that of the monkey.

As described earlier in *Monkey behavior during a color-judgment task*, the magnitude of the psychometric thresholds varied depending on their position on the chromaticity diagram (Fig. 5, C and D). If the activity of TE neurons affects the color judgment of a monkey, we would expect that there would be some correlation between the changes in the neurometric and psychometric thresholds across the color space. To test this possibility, we examined whether the neurometric and psychometric thresholds exhibit correlated variation across different positions on the CIE-xy chromaticity diagram. In Fig. 9, A and B, neurometric thresholds (blue lines) obtained at various positions on the chromaticity diagram are superimposed on the psychometric thresholds (red lines) obtained simultaneously. They illustrate that both thresholds are relatively short around white but long around cyan and it appears that both thresholds change in a similar manner, depending on their position on the chromaticity diagram.

Although the relationships between the neurometric and psychometric thresholds are shown in Fig. 8G, it is hard to evaluate the dependence on color in this figure because the data were not sorted according to their positions on the chromaticity diagram. Therefore to systematically examine this issue, we first binned the data and then computed the correlation. To bin the data, we divided the chromaticity diagram into 10 areas (Fig. 9C, inset) and computed the respective averages of both thresholds in each area. These 10 areas included 9 that divided each edge of the color triangle into equal parts, plus the region...
around white. We then classified each threshold into one of the 10 areas based on where the center of the sample color set was situated and computed the geometric mean. Finally, we tested whether there was a correlation between the two thresholds across different areas in the color space. Figure 9, C and D illustrates that in both monkeys there was a significant correlation between the two threshold values (monkey Y, \( r = 0.892, P = 0.01, n = 9 \); monkey R, \( r = 0.882, P < 0.01, n = 9 \); both, \( r = 0.88, P < 0.001, n = 10 \)), which is consistent with the idea that there is a close relationship between the activity of TE neurons and the monkeys’ color discrimination behavior. Moreover, most of the data points in Fig. 9, C and D were located below the diagonal line, reflecting the fact that the neurometric threshold tended to be larger than the psychometric threshold, as described earlier.

**Choice probability**

The results described so far indicate that there is a correlation between the color-discrimination thresholds of TE color-selective neurons and those of the monkeys. If the activities of these neurons actually contribute to the color perception of monkeys, we would expect that in a trial in which the neural response is relatively strong, the monkey would tend to choose the target associated with color #7 (color #7-choice), which is the preferred color of the recorded neuron, and vice versa; and, if so, we would further expect that there would be a correlation between the trial-to-trial fluctuation in the neural responses and the color judgment of the monkey. To examine this correlation, we computed the CP (see METHODS), which will be >0.5 if there is the expected correlation between neuronal activity and behavior. Because behavioral fluctuation is most clearly observed for the center color of the sample color set, we first computed the distribution of CPs for trials in which color #4 was presented as the sample color (Fig. 10A). Overall, the

**FIG. 7.** Computation of the neurometric threshold for the same neuron shown in Fig. 6. A: actually recorded responses of the pref-neuron to each sample color (solid line) and those of the hypothetical antineuron (broken line); error bars are SD. Responses of the antineuron are mirror reversals of the responses of the pref-neuron. Data points are shifted horizontally to improve visibility of data points. B: neurometric function (solid line) based on the receiver-operating-characteristic (ROC) values for each sample color. ROC analysis was conducted to compute the probability that the ideal observer makes a color #7-choice based on the response distributions for each sample color. The resultant ROC values represent the probability of the color #7-choice. The neurometric threshold (arrow) was calculated in the same way as the psychometric threshold.

**FIG. 8.** Comparison of the neurometric and psychometric functions. A–F: neurometric functions (crosses, solid line) computed from the responses of the 6 example neurons plotted together with simultaneously recorded psychometric functions (circles, broken line). Neurons in A and D illustrate examples in which neuronal responses exhibited greater sensitivity to the sample colors than the monkey. Those in B and E illustrate examples in which neural sensitivity was comparable to the monkey. Those in C and F illustrate examples in which neurons exhibit less sensitivity than the monkey. G: relationship between the neurometric threshold (abscissa) and the simultaneously recorded psychometric threshold (ordinate). The thresholds are in units of the CIE-xy chromaticity diagram. Open circles and filled squares represent monkeys Y and R, respectively. The histogram in the inset shows the distribution of the difference between the neurometric and psychometric thresholds on a log scale. Open and filled bars represent the data from monkeys Y and R, respectively; the triangle indicates the average of the difference.
mean CP for the two monkeys was 0.522, which was significantly >0.5 \( (n = 85, \text{Wilcoxon test, two-tailed, } P < 0.001) \). This was also true for each individual monkey (monkey Y, \( n = 57, \text{mean} = 0.516, P < 0.05 \); monkey R, \( n = 28, \text{mean} = 0.535, P < 0.05 \)).

We next applied the same analysis to other sample colors. Figure 10B shows the CPs for each neuron tested for each sample color. Because CPs were computed only when the monkey made both color #7-choices and color #1-choices more than 10 times, the numbers of neurons included in the samples differed, depending on the sample color. For all sample colors except #7, the mean CP (horizontal bar) tended to be >0.5. In particular, the mean CPs for colors #3, #4, and #5 were significantly >0.5 (asterisks, Wilcoxon test, two-tailed, \( P < 0.05 \)).

![Distribution of choice probability (CP). A: distribution of CPs for sample color #4 across the recorded neurons. Filled bars represent the neurons with CPs that are significantly different from 0.5 (permutation test, \( P < 0.05 \)). The triangle indicates the mean CP, which is significantly larger than 0.5 (Wilcoxon test 2-tailed, \( P < 0.01 \)). B: CPs for each neuron tested for each sample color. Each circle in the column represents a CP from one neuron. The numbers of neurons included in the sample data differ depending on the sample color because the CP was computed only when the monkey made both color #7-choices and color #1-choices more than 10 times. Filled circles indicate CPs that are significantly different from 0.5 (permutation test, \( P < 0.05 \)); circles are jittered horizontally to avoid overlap. Horizontal bars indicate the mean CPs for each sample color and the asterisks indicate that the average CP is significantly different from 0.5 (Wilcoxon test 2-tailed, \( P < 0.05 \)). C: distribution of the grand choice probability (GCP) across the 87 neurons analyzed. Filled bars represent neurons with a GCP that is significantly different from 0.5 (permutation test, \( P < 0.05 \)). The triangle indicates the mean of GCP, which was significantly larger than 0.5 (Wilcoxon test 2-tailed, \( P < 0.05 \)).](download.springer.com/static/10220_32_247.png)
0.05). We also found that there was consistency with respect to CP among the individual neurons across the different sample colors (Supplemental Fig. S1).1 The number of trials for color #7 was very small, making the results for this color unreliable.

To obtain a representative CP value for each neuron, we combined a given neuron’s responses to different sample colors into a single CP value. For this purpose, the neural responses used to compute the CP for each sample color were normalized by z-scoring, then combined to generate the “grand” response distribution and sorted according to the monkey’s choice. The CP was then calculated in the same way as regular CPs to obtain the “grand choice probability (GCP).” Figure 10C shows the distribution of the GCPs. The mean of the GCPs was 0.517, which is significantly >0.5 (n = 87, Wilcoxon test, two-tailed, P < 0.001) and, with one exception, all significant GCPs were >0.5. Thus there appears to be a weak but reliable positive correlation between trial-to-trial neural responses to a sample color and a monkey’s color judgment. In other words, the monkeys tended to make the color #7-choice in trials where a neuron responded strongly.

Relationships between each neuron’s ability to discriminate color and the choice probability

So far, we have analyzed the relationship between the activity of TE color-selective neurons and the monkeys’ color judgment using two different measures: 1) the neurometric threshold, which when compared with the psychometric threshold, is a measure of each neuron’s ability to discriminate color; and 2) the CP, which is a measure of the contribution of each neuron to the monkeys’ judgment. We found that, with both measures, there was a positive correlation between the activity of the neurons and the monkeys’ color judgment (Figs. 9, C and D and 10). So what is the relationship between these two measures in individual neurons? One possibility is that neurons showing strong color discrimination are especially engaged in color-judgment behavior (Britten et al. 1996; Celebrini and Newsome 1994; Purushothaman and Bradley 2005; Uka and DeAngelis 2004). If that is the case, we would expect that there is a positive correlation between the neural sensitivity to sample colors and the CP. Another possibility is that many neurons with differing abilities to discriminate color contribute equally to the color judgment. If this is the case, there may be no correlation between the neural sensitivity to color and CP. We tested which of these alternatives is more plausible by analyzing the correlation between neural sensitivity, the inverse of the neurometric threshold, and GCP across the entire population of neurons. We normalized neural sensitivity taking into account the variation in color-discrimination ability that reflected the color’s position on the chromaticity diagram (Fig. 9, C and D). To do this, the neural threshold for each neuron was divided by the average neural threshold for each color area containing the center of the sample color set. Figure 11 shows that there was no significant correlation between this normalized neural sensitivity and GCP (all neurons: n = 83, r = 0.0578, P = 0.604; significant neurons: n = 17, r = 0.196, P = 0.45). When the neural threshold for each neuron was normalized to the simultaneously obtained psychometric threshold, the result was the same and there was no

1 The online version of this article contains supplemental data.
period (Wilcoxon test, two-tailed, \( P < 0.05 \)) from 100 to 450 ms after sample color onset, then declined to near 0.5 toward the end of the sample color presentation. These results suggest that the neural activity during nearly the entire period contributed to the color judgment, although the activity in the early period after sample onset, when GCP was the largest, may have been most important.

**DISCUSSION**

Although it is well established that lesioning or inactivation of area TE in monkeys degrades their ability to discriminate colors (Buckley et al. 1997; Dean 1979; Heywood et al. 1995; Horel 1994; Huxlin et al. 2000), ours is the first study in which the relationship between the activity of TE color-selective neurons and color-discrimination behavior was systematically examined. We found that the color-discrimination threshold computed from the neural responses was, on average, higher than the behavioral threshold and that variation in the neural threshold across the color space corresponded well with variation in the behavioral threshold. We also found that there is a significant correlation between the trial-to-trial fluctuation in neural activity and the monkeys’ color judgment, although there is little correlation between the neural sensitivity for color discrimination and the magnitude of the CP. These results suggest that a large population of color-selective TE neurons with differing color sensitivities—rather than a specific subset of neurons with particularly high color sensitivity—contribute to color discrimination.

**Comparison of neuronal activities and the monkeys’ behavior**

Ideal-observer analysis has previously been applied to the visual cortical areas of monkeys to investigate the quantitative relationship between neuronal activity and the perception of the direction and speed of motion and of depth (Britten et al. 1992; Celebrini and Newsome 1994; Heuer and Britten 2004; Nienborg and Cumming 2006; Uka and DeAngelis 2003). In those studies, the average neural performance was generally comparable to or better than that of the monkey. In the present study, by contrast, the neural sensitivity for color discrimination was less than that of the monkey.

There are differences between the temporal properties of the visual stimuli used in the present study and those earlier ones that may account for the comparatively low neural sensitivity we observed. The visual stimuli used in many of the earlier studies consisted of dynamically changing random dots that appeared and disappeared during the stimulus presentation; that is, the visual stimuli were different in every monitor frame. By contrast, our visual stimuli were uniformly colored figures that remained constant during the entire stimulus presentation. This difference suggests that temporal integration of stimulus information during the stimulus presentation may have been more important in the earlier studies using dynamic stimuli than in the present one. In fact, in the present study, neural sensitivity does not improve clearly if the neural signals are integrated for \( >200 \) ms (Supplemental Fig. S3). Our monkeys could make judgments using only signals from an early phase of the stimulus presentation. To test this possibility, we computed the time course of the neural sensitivity, which was
normalized to the behavioral sensitivity in the same session (Supplemental Fig. S4). We found that neural sensitivity was greatest during the early half of color presentation and then gradually declined in the latter half. However, even the peak value of the population average of the neural sensitivity (0.65) was lower than that of the behavioral sensitivity (corresponding to 1). Thus even when we consider only the peak, neurons still showed less color sensitivity than did the monkeys’ behavior.

One possible reason for the lower neural sensitivity is that the sample color set may not always have been selected based on the position on the chromaticity diagram where the sensitivity of the neuron under study was highest. The color selectivity of a neuron can be defined two-dimensionally on the chromaticity diagram (e.g., Fig. 3, B–D) in the directions of both hue and saturation and the steepest slope may reside in the direction of saturation or in the direction of a hue. Such ambiguity in the optimal direction was less likely to occur in the earlier experiments, where neural sensitivity to direction of motion or stereoscopic disparity was examined. In those cases, neural selectivity could be regarded basically as one-dimensional, so the optimal direction to test neural sensitivity would be more clearly determined.

Another possibility is that lower neural sensitivity reflects the difference in task demand (fine discrimination vs. coarse discrimination). It is reported that neurometric thresholds are larger than psychophysical thresholds during fine depth-discrimination tasks, even when the stimulus is precisely matched to the preference of the neurons (Prince et al. 2000; Uka and DeAngelis 2006). Our present task required monkeys to make a threshold color discrimination, which might have resulted in lower neural sensitivity.

Comparison of the abilities of neurons and monkeys to discriminate different colors in the color space

We found that variations in the abilities of neurons to discriminate color positively correlated with the monkeys’ abilities in the color space (Fig. 9, C and D). This suggests that if we consider a color pair separated by a certain distance on the CIE-xy chromaticity diagram, the easier the discrimination is for the neurons, the easier the discrimination will be for the monkey. This strongly supports the idea that there is an association between the activities of the recorded IT neurons and the monkeys’ color perception. They also suggest that the correlation of the two thresholds is also true for other color spaces, given that projection from one color space to another distorts neurometric and psychometric thresholds in the same way.

Source of correlation between neural activity and behavior

A significant CP suggests that fluctuation of the color signal in TE can cause fluctuation in color judgment. However, we need to consider the possibility that a top-down signal from a higher area, where the behavioral decision is made, may have led to the significant CP. In other words, the CP observed in area TE might reflect the outcome of that decision, but not the cause, although this possibility is highly unlikely. When we analyzed the time courses of neuronal responses and GCP (Fig. 12), the difference in the neural activity associated with the monkeys’ color judgment and GCP arose about 100 ms after the onset of sample color presentation, which is near the response latency of TE neurons. It is hard to explain how such an early rise in neuronal activity associated with the monkeys’ color judgment could be based only on a feedback signal from higher areas. Another possibility—that small eye movements during sample presentation generated the significant CP—was excluded by our supplemental analysis (Supplemental Fig. S5). We therefore conclude that the CPs we obtained reflect genuine correlations between the activities of TE color-selective neurons and color judgments in the monkey.

Relationship between the color sensitivity and choice probability of individual neurons

The average GCP of 0.517 is lower than has been seen in similar analyses carried out previously. In addition, we did not find a correlation between neural discrimination sensitivity and CP, as was seen in earlier studies. One possible cause of this difference is the task design. In most of the earlier studies, the monkeys had to discriminate the polarity of the visual stimulus; for example, one direction versus the opposite direction or a crossed disparity versus an uncrossed disparity. In the present study, by contrast, the monkeys had to discriminate a small difference along a continuum of visual stimuli. In such a situation, the brain may need to use more neurons to make a judgment than are needed when only polarity is discriminated. This would make the relative contribution of each individual neuron smaller in the present experiment. Consistent with that idea, in a study of speed discrimination, the average CP was relatively low (0.524) (Liu and Newsome 2005). By comparison, a study using a fine direction-discrimination task (Purushothaman and Bradley 2005) yielded a CP (0.55) that was higher than that in the present study and also showed that the monkey’s decision depended on the activities of most sensitive neurons. However, they used a fixed reference stimulus that became the border for making a judgment, whereas our color stimulus set changed for every neuron and the color border for judgment changed in each session. Consequently, their monkeys likely constructed stronger connections between the more sensitive neurons and those that read out the signal to make behavioral judgments than ours, which could account for the difference in the results.

In the present study, we found no correlation between the neural sensitivity and CP. Based on their simulation of the population activities of model MT neurons, Shadlen et al. (1996) suggested that in addition to the connection weight between the recorded neurons and the neurons in the downstream areas, systematic variation in the correlation of activities across neurons is important for generation of a CP’s dependence on neural sensitivity. As mentioned earlier, our task design differed from most of the earlier designs and this may have caused differences in the pattern of neural correlations between our sample neurons and those in previous studies, although we did not measure the correlation of neural activities in the present study.

Finally, it is important to consider how other areas within and outside the IT cortex may contribute to color discrimination. Although IT or TE lesions cause significant deficits in color discrimination, they do not completely eliminate a monkey’s ability to discriminate color (Dean 1979; Huxlin et al.
in addition, recent studies have shown that other IT subregions are activated by color stimuli (Conway et al. 2007; Tootell et al. 2004; Yasuda and Komatsu 2005). This suggests large ensembles of neurons scattered within and outside the IT cortex may contribute to color discrimination, which would make the contribution of individual TE neurons to color judgment small.

ACKNOWLEDGMENTS

We thank T. Ogawa and M. Togawa for technical assistance and I. Fujita, I. Minami, and N. Goda for valuable comments on the manuscript. Present address of T. Matsumora: The Zanvyl Krieger Mind/Brain Institute, Johns Hopkins University, 338 Krieger Hall, Baltimore, MD 21218.

GRANTS

This work was supported by a Japanese Grant-in-Aid for Scientific Research (B) and Scientific Research on Priority Areas Grant 17022040 (“System study on higher-order brain functions”) from Ministry of Education, Culture, Sports, Science and Technology of Japan.

REFERENCES


